



Relationship between foramen magnum position and locomotion in extant and extinct hominoids



Dimitri Neaux^{a,*}, Thibaut Bienvenu^{b,c}, Franck Guy^b, Guillaume Daver^b,
Gabriele Sansalone^{a,d,e}, Justin A. Ledogar^a, Todd C. Rae^f, Stephen Wroe^a,
Michel Brunet^{b,c}

^a Function, Evolution and Anatomy Research Lab, School of Environmental and Rural Science, University of New England, Bldg CO2, Armidale, NSW 2351, Australia

^b Institut de Paléoprimatologie, Paléontologie Humaine: Evolution et Paléoenvironnements – UMR CNRS 7262, Université de Poitiers, Poitiers, Bât B35, 6 Rue Michel Brunet, 86073, France

^c Collège de France, Chaire de Paléontologie Humaine, 3 Rue D'Ulm, 75231 Paris, France

^d Department of Sciences, Roma Tre University, Largo San Leonardo Murialdo 1, I-00146 Rome, Italy

^e Center for Evolutionary Ecology, Largo San Leonardo Murialdo 1, I-00146 Rome, Italy

^f Centre for Research in Evolutionary, Social and Inter-Disciplinary Anthropology, University of Roehampton, Holybourne Avenue, London, SW15 4JD, United Kingdom

ARTICLE INFO

Article history:

Received 3 February 2017

Accepted 20 July 2017

Keywords:

Basicranium

Bipedalism

Hominin

Masticatory apparatus

ABSTRACT

From the Miocene *Sahelanthropus tchadensis* to Pleistocene *Homo sapiens*, hominins are characterized by a derived anterior position of the foramen magnum relative to basicranial structures. It has been previously suggested that the anterior position of the foramen magnum in hominins is related to bipedal locomotor behavior. Yet, the functional relationship between foramen magnum position and bipedal locomotion remains unclear. Recent studies, using ratios based on cranial linear measurements, have found a link between the anterior position of the foramen magnum and bipedalism in several mammalian clades: marsupials, rodents, and primates. In the present study, we compute these ratios in a sample including a more comprehensive dataset of extant hominoids and fossil hominins. First, we verify if the values of ratios can distinguish extant humans from apes. Then, we test whether extinct hominins can be distinguished from non-bipedal extant hominoids. Finally, we assess if the studied ratios are effective predictors of bipedal behavior by testing if they mainly relate to variation in foramen magnum position rather than changes in other cranial structures. Our results confirm that the ratios discriminate between extant bipeds and non-bipeds. However, the only ratio clearly discriminating between fossil hominins and other extant apes is that which only includes basicranial structures. We show that a large proportion of the interspecific variation in the other ratios relates to changes in facial, rather than basicranial, structures. In this context, we advocate the use of measurements based only on basicranial structures when assessing the relationship between foramen magnum position and bipedalism in future studies.

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1. Introduction

1.1. Bipedalism and foramen magnum position

When compared to other hominoids, extant and extinct hominins are characterized by a derived anterior position of the foramen

magnum, highlighting a reorganization of the surrounding basicranial structures (Dart, 1925; Schultz, 1942; Dean and Wood, 1981; Kimbel and Rak, 2010). The discoveries of *Sahelanthropus tchadensis* (Brunet et al., 2002; Guy et al., 2005; Zollikofer et al., 2005) and *Ardipithecus ramidus* (White et al., 1994; Suwa et al., 2009; Kimbel et al., 2014), both of which exhibit an anteriorly placed foramen magnum, show that this conformation was acquired by at least the late Miocene. Previous studies suggested that the anterior position of the foramen magnum in hominins is related to a habitual bipedal

* Corresponding author.

E-mail address: dimitrineaux@gmail.com (D. Neaux).

locomotor behavior (Broca, 1872; Topinard, 1878; Dart, 1925; Broom, 1938; Le Gros Clark, 1955; Tobias, 1967). However, the functional relationship between foramen magnum position and bipedal locomotion remains unclear (Suwa et al., 2009; Ruth et al., 2016). This is because the anterior position of the foramen magnum and obligate bipedalism are only displayed by humans among extant hominoids. Morphofunctional comparative studies of extant primate cranial base structures are thus inherently limited by the unique nature of the foramen magnum position and locomotor behavior of *Homo sapiens* (see Cartmill, 1990).

To address this challenge, Russo and Kirk (2013) tested the hypothesis that an anteriorly positioned foramen magnum is related to bipedalism through a comparison of basicranial anatomy between bipeds and quadrupeds belonging to three mammalian clades: marsupials (e.g., bipedal kangaroos and wallabies vs. quadrupedal marsupials), rodents (e.g., bipedal kangaroo rats and jerboas vs. quadrupedal rodents), and primates (humans vs. other hominoids). They used three ratios to describe the position of the foramen magnum relative to several splanchnocranial structures (i.e., anterior margin of the temporal fossa, posterior aspect of the last molar crown, and midline posterior aspect of hard palate). The results of Russo and Kirk (2013) demonstrated that, when compared to their quadrupedal relatives, bipedal marsupials, rodents, and primates have a foramen magnum that is more anteriorly positioned (see also Brunet et al., 2002; Suwa et al., 2009; Kimbel and Rak, 2010).

Ruth et al. (2016) challenged the findings of Russo and Kirk (2013), arguing that the chosen ratios did not accurately relate to foramen magnum position, but instead correspond to changes in other cranial structures. Ruth et al. (2016) notably asserted that these ratios are more influenced by masticatory apparatus position and size rather than foramen magnum position. Recently, Russo and Kirk (2017) responded to these criticisms by quantifying the position of the foramen magnum using a new metric based on the position of the sphenoccipital synchondrosis. This new ratio has the advantage of being based on basicranial structures only and does not take into account features related to the masticatory apparatus. Using this metric, Russo and Kirk (2017) confirmed their previous results (Russo and Kirk, 2013), stating that a relationship exists between foramen magnum position and bipedalism in mammals.

1.2. Objectives of this study

Objective #1 In this context, our first objective is to assess if the use of a more comprehensive sample of extant hominoid specimens, including extant species for which the ratios have not been measured yet (e.g., *Pan paniscus*, *Gorilla beringei*, *Pongo abelii*, *Symphalangus syndactylus*), allows corroborating Russo and Kirk (2013, 2017) findings. We use linear measurements and the same ratios in order to facilitate comparison of our results with those of previous analyses. We first test the hypothesis (hypothesis 1) that ratios can distinguish humans from non-bipedal extant hominoids. We compute and compare the ratios for *H. sapiens* and 18 other species belonging to *Pan*, *Gorilla*, *Pongo*, *Hylobates*, *Nomascus*, *Symphalangus*, and *Hoolock*. If hypothesis 1 is rejected, the findings of Russo and Kirk (2013, 2017) will not be corroborated when a larger taxonomic group is included in the study. If the results are consistent with hypothesis 1, our study will confirm that the ratios proposed by Russo and Kirk (2013, 2017) distinguish bipedal (*H. sapiens*) from non-bipedal extant hominoids.

Objective #2 Russo and Kirk (2013, 2017) also suggested that their ratios may be good proxies with which to appraise bipedalism in fossil hominins (Ross and Henneberg, 1995; Nevell and Wood,

2008; Kimbel and Rak, 2010). We compute the ratios proposed by Russo and Kirk (2013, 2017) in a sample of extinct hominins possessing a wide variety of basicranial shapes in order to appraise this statement. We test the hypothesis (hypothesis 2) that the values of the ratios can distinguish between extinct hominins and non-bipedal extant hominoids. A rejected hypothesis 2 will indicate that factors, other than locomotor behavior, are likely to play a part in the ratio values. If the results are in line with hypothesis 2, our study will confirm that the studied ratios are good descriptors of bipedalism in extinct hominins.

Objective #3 As the ratios defined by Russo and Kirk (2013) have been criticized by Ruth et al. (2016), who asserted that they are likely to be affected by the masticatory apparatus, we test the hypothesis (hypothesis 3) that the ratios mainly describe variation in foramen magnum position rather than changes in facial structures. We quantify the variation in the structures related to the studied ratios using geometric morphometric methods on 3D homologous landmarks. If a significant proportion of the variation is related to landmarks located on the face, hypothesis 3 will be rejected and the masticatory apparatus is likely to influence the ratios that include facial features. If most of the variation is related to basicranial landmarks, notably basion, results will be in line with hypothesis 3.

2. Material and methods

2.1. Studied sample

The sample consists of 171 crania, including 157 extant hominoid specimens belonging to 19 different species (Table 1). The remaining crania belong to extinct taxa. All extant individuals were determined to be adults based on the full eruption of the third molars. These specimens are housed in the American Museum of Natural History (New York, USA), the National Museum of Natural

Table 1

Number of specimens for each species included in the studied sample, including catalog numbers for fossil specimens.

Species	Number	Fossil specimens
<i>Homo sapiens</i>	24	
<i>Pan troglodytes</i>	26	
<i>Pan paniscus</i>	13	
<i>Gorilla gorilla</i>	23	
<i>Gorilla beringei</i>	11	
<i>Pongo pygmaeus</i>	19	
<i>Pongo abelii</i>	5	
<i>Hylobates lar</i>	3	
<i>Hylobates muelleri</i>	3	
<i>Hylobates agilis</i>	3	
<i>Hylobates klossii</i>	3	
<i>Hylobates alibarbis</i>	2	
<i>Hylobates moloch</i>	3	
<i>Hylobates pileatus</i>	2	
<i>Nomascus leucogenys</i>	3	
<i>Nomascus concolor</i>	4	
<i>Nomascus gabriellae</i>	1	
<i>Symphalangus syndactylus</i>	7	
<i>Hoolock hoolock</i>	2	
<i>Sahelanthropus tchadensis</i>	1	TM 266-01-060-1
<i>Australopithecus africanus</i>	1	STS 5
<i>Paranthropus aethiopicus</i>	1	KNM-WT 17000
<i>Paranthropus boisei</i>	2	KNM-ER 406, OH 5
<i>Homo habilis</i>	1	KNM-ER 1813
<i>Homo erectus</i>	3	KNM-ER 3733, KNWT-15000, D2700
<i>Homo heidelbergensis</i>	2	Kabwe 1, Petralona 1
<i>Homo neanderthalensis</i>	2	La Ferrassie 1, La-Chapelle-aux-Saints 1
Early <i>Homo sapiens</i>	1	Skhul V

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